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Abstract

Using magnetoencephalography (MEG), the current study examined gamma activity associated with language prediction. Participants read high- and low-constraining sentences in which the final word of the sentence was either expected or unexpected. Although no consistent gamma power difference induced by the sentence-final words was found between the expected and unexpected conditions, the correlation of gamma power during the *prediction* and the *activation* intervals of the sentence-final words was larger when the presented words matched with the prediction compared to when the prediction was violated or when no prediction was available. This suggests that gamma magnitude relates to the match between predicted and perceived words. Moreover, the expected words induced activity with a slower gamma frequency compared to that induced by unexpected words. Overall, the current study establishes that prediction is related to gamma power correlations and a slowing of the gamma frequency.

1. Introduction

Language processing is predictive in the sense that context influences the state of the language processing system prior to the actual word input (Kuperberg & Jaeger, 2016). EEG and MEG techniques are ideal for studying prediction as they can capture the rapid change of brain states. A number of event-related potential/field (ERP/F) studies have shown that comprehenders anticipate different aspects of upcoming information such that the violation of the prediction elicits detectable brain responses (e.g. DeLong, Urbach, & Kutas, 2005; Molinaro, Barraza, & Carreiras, 2013; Van Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005). Recently, several studies measured the ERPs during the anticipation period preceding the word input. They found that highly constraining contexts produced larger negativities compared to less constraining contexts (Freunberger & Roehm, 2017; Grisoni, Miller, & Pulvermüller, 2017; León-Cabrera, Rodríguez-Fornells, & Morís, 2017; Maess, Mamashli, Obleser, Helle, & Friederici, 2016).

The aforementioned studies focused on evoked responses, which mainly reflect stimulus-locked brain activity. However, a part of the event-induced activity is not stimulus-locked to a certain event, e.g. oscillatory activity which is not phase-aligned by the event. Neural oscillations are thought to play a crucial role in linking spatially distributed representations and functionally related brain regions (Varela, Lachaux, Rodriguez, & Martinerie, 2001; Engel, Fries, & Singer, 2001; Fries, 2005). Both slow (< 30 Hz) and fast (> 30 Hz) oscillatory activities have been reported during language prediction. For instance, increased theta power (Rommers, Dickson, Norton, Wlotko, & Federmeier, 2016) and decreased beta power (Wang, Jensen, et al., 2012) have been reported when predictions were violated. Moreover, several studies found that highly constraining contexts induced a theta power increase (Dikker & Pylkkänen, 2013; Piai et al., 2016) and an alpha/beta power

suppression relative to less constraining contexts (Piai, Roelofs, & Maris, 2014; Piai, Roelofs, Rommers, & Maris, 2015; Rommers et al., 2016; Wang, Hagoort, & Jensen, 2017) during the anticipatory time window. These results indicate that language prediction triggers the engagement of a large-scale language network. Moreover, we found that the frontal gamma and temporal lobe alpha oscillations correlated negatively when the prediction was strong, indicating a functional connectivity between different nodes in the language network (Wang, Hagoort, & Jensen, 2017).

Gamma activity (> 30 Hz) has been reported in response to visual or auditory word presentations. For instance, increased gamma power (around 40 Hz) was observed for expected words (Hald, Bastiaansen, & Hagoort, 2006; Monsalve, Pérez, & Molinaro, 2014; Peña & Melloni, 2012; Penolazzi, Angrilli, & Job, 2009; Rommers, Dijkstra, & Bastiaansen, 2013; Wang, Zhu, & Bastiaansen, 2012) but not for unexpected words (but see Hagoort, Hald, Bastiaansen, & Petersson, 2004). Moreover, increased long-range gamma phase-synchronization was found for high- compared to low-constraining contexts both before and after a target word was presented (Molinaro et al., 2013). Therefore, increased gamma activity has been suggested to reflect the match between the received linguistic input and the pre-activated lexical representations (Lewis, Wang, & Bastiaansen, 2015). This notion is consistent with the view that synchronization in the gamma band plays a role in binding together information from external sensory input and internal top-down processes (Tallon-Baudry & Bertrand, 1999). For instance, increased gamma power was found for stimuli that matched with the representations stored in long-term and working memory (Herrmann, Lenz, Junge, Busch, & Maess, 2004; Herrmann & Mecklinger, 2001; Osipova et al., 2006), indicating that the successful matching between external input and internal representation induces gamma power increase.

However, associating increased gamma power to *confirmed predictions* is in contradiction to the proposal that gamma activity reflects prediction error (Arnal & Giraud, 2012; Friston, Bastos, Pinotsis, & Litvak, 2015) in the context of the predictive coding framework (Clark, 2013; Friston, 2011; Rao & Ballard, 1999). According to this framework, the brain infers the possible causes of sensory input based on prior experiences. These generated hypotheses are then compared to incoming sensory information. Prediction error reflects the difference between the top-down expectation and incoming sensory inputs. In the case where no strong prediction of upcoming input is available, the bottom-up input is unpredicted and thus a prediction error will be generated as well. The prediction error is propagated forward throughout the cortical hierarchy via gamma activity, with unexpected stimuli producing greater gamma power. Supporting evidence primarily comes from visual (Bastos et al., 2015) and auditory (Arnal, Wyart, & Giraud, 2011; Todorovic, van Ede, Maris, & de Lange, 2011) perception studies, but experimental evidence from higher-order cognitive domains remains elusive.

In the current study, we presented sentences with high-constraining or low-constraining contexts. At the same time, the sentence-final word (SFW) was either congruent or incongruent relative to the context. Consequently, the SFWs were expected in the high-constraining and congruent condition but not in the other three conditions: high-constraining incongruent, low-constraining congruent, low-constraining incongruent. Note that the same dataset was analyzed in our previously published study (Wang, Hagoort, & Jensen, 2017). However, the present study focused on the gamma activity associated with prediction using very different approaches. The first aim of the current study was to examine the gamma power induced by the expected (the congruent SFWs in the high-constraining contexts) and

unexpected (the incongruent SFWs in the high-constraining contexts as well as the SFWs in the low-constraining contexts) words. If gamma power relates to the agreement between the pre-activated words and the words that are actually presented, the gamma power induced by the expected words in the high-constraining contexts should be higher than the power induced by the unexpected words in the other three conditions. On the contrary, if gamma power relates to prediction error (i.e. the mismatch between prediction and bottom-up input), the gamma power should be higher for the unexpected words in both the high- and low-constraining contexts than the expected words in the high-constraining context.

In addition to examining the gamma power induced by the sentence-final words, we were also interested in how the gamma activity in response to the presented words related to the gamma activity associated with the prediction of those words. In the working memory literature, it has been shown that the spatial/temporal pattern of brain activity during encoding and retrieval of remembered items is highly similar (e.g. Michelmann, Bowman, & Hanslmayr, 2016; Staudigl, Vollmar, Noachtar, & Hanslmayr, 2015; Wolff, Jochim, Akyurek, & Stokes, 2017) and that content-specific information can be decoded from gamma activity (Polanía, Paulus, & Nitsche, 2012; Zhang et al., 2015). By correlating the gamma band activity between the activation and prediction intervals across trials, we would be able to further test whether the magnitude of the gamma activity relates to item-specific predictions. We hypothesized that a word associated with high gamma power in the activation time window will induce high gamma power in the prediction time window within the same trial. Therefore, if gamma activity indeed reflects the match between predicted and perceived words, the correlation of the gamma power between the activation and prediction periods should be greater in the high-constraining congruent condition than the high-constraining incongruent conditions or the low-constraining conditions, as the item-specific pre-activation

is only made and matched in the high-constraining congruent condition.

Finally, we quantified the frequency content of the gamma activity induced by the expected (in the high-constraining congruent condition) and unexpected (in the other three conditions) words to test whether there was a change in gamma frequency. Slower and faster gamma activities have been associated with prospective memory retrieval and maintenance of recent sensory information respectively in rat hippocampal recordings (Colgin & Moser, 2010). In the current study, we expected a slower gamma frequency for the expected words in the high-constraining congruent condition (as the highly predictive contexts could facilitate prospective retrieval) and a faster gamma frequency for the unexpected words in the other three conditions (because they might be maintained temporarily in order to be integrated into the contexts).

2. Methods

The participants, stimuli, procedure and data acquisition have been reported more extensively in (Wang et al., 2017).

2.1. Participants

Thirty-four right-handed native Dutch speakers (mean age 24 years old, range 20 – 35; 13 males) served as paid volunteers. They had normal or corrected-to-normal vision. None of them had dyslexia or any neurological impairment. They signed a written consent form according to the Declaration of Helsinki. The data of one male and one female were excluded because of severe metal-related artifacts from dental work. The final set of participants therefore consisted of 32 participants (mean age: 24, range 20 – 35; 12 males).

2.2. Stimulus

We constructed 240 Dutch sentence pairs, each pair ending with the same sentence-final word (SFW, see Table 1 for some examples). Each sentence pair differed in only one word, which preceded the SFW by at least two words. The differing words in each sentence pair created either highly constraining (HC) or low constraining (LC) contexts, so that the SFW could be predicted in the HC context whereas it could not be predicted in the LC context. A cloze-probability test was conducted to quantify the sentence constraints in two groups of participants who did not participate in the MEG study. The semantic constraint of the context was quantified by the percentage of participants who filled in the most common word for each sentence. The cloze test showed that the HC sentences had higher contextual constraints than the LC sentences: Mean (SD) = 86% (11%) and 28% (10%), respectively; $t_{(478)} = 62.27$, $p < .001$. The cloze probability of the SFW was quantified by the percentage of the participants who completed the sentence with that word. The SFW had higher cloze probability in the HC sentences (86%) than in the LC sentences (6%). The mean sentence length was 8 words (range: 5 – 15 words).

Insert Table 1 here

We also manipulated the semantic congruence of the SFWs by replacing the expected words with words that made the sentences incongruent in both the HC and LC contexts. A sentence plausibility test was conducted to quantify the semantic congruency in a different group of participants. They were asked to rate the plausibility of each sentence on a scale from 1 (highly implausible) to 7 (highly plausible). The Congruent (C) sentences were rated to be more plausible than the IC sentences. Also, the plausibility difference between the IC and C sentences was larger for the HC than for the LC sentences. The mean and SD of the ratings in the four conditions were: HC/C: 6.49 (0.09); HC/IC: 1.59 (0.10); LC/C: 5.79 (0.12); LC/IC:

1.94 (0.12). Moreover, the IC and C words were matched on word category, animacy, word frequency, and word length. The four conditions of all 240 sentences were distributed among four lists with a Latin square design, so that each participant read 60 sentences of the same condition.

2.3. Procedure

Participants were tested individually in a magnetically shielded room. They were seated in a comfortable chair under the MEG helmet, facing a projected screen at approximately 80 cm distance. The stimuli were presented in grey color on a black background on the screen, with a font size of 36 for the words and of 30 for the probe statements. A trial started with a blank screen (duration 1600 ms), followed by a sentence that was presented word by word. Each word was presented for 200 ms, with an inter-stimulus interval of 800 ms. The last word ended with a period. After 1600 ms, the participants either saw a statement (20% of trials) or a 'NEXT' signal. For the trials in which participants saw a statement following the sentence, they were required to judge the accuracy of the statement by pressing one of two buttons to ensure that they had read for comprehension. In the other trials, the participants were instructed to press a third button. All responses were required to be delivered within 5000 ms. After a response, the next trial began. Participants were asked not to move or blink when individual words appeared, but they were encouraged to blink during the presentation of the questions.

Participants read one list of 240 sentences in a pseudo-random order. No more than three sentences of the same condition were presented in succession. The 240 sentences in one list were divided into 12 blocks (24 trials per block), with each block lasting about five minutes. Between each block there was a small break, after which participants could start the

next block by informing the experimenter. The whole experiment took about 1.5 hours, including participants' preparation, instructions and a short practice session consisting of 12 sentences.

2.4. Data acquisition

MEG signals were recorded with 275 axial gradiometers CTF Omega System. In addition, horizontal and vertical electrooculogram (EOG) as well as electrocardiography (ECG) were recorded to later discard trials contaminated by eye movements, blinks and heart beats. The ongoing MEG and EOG signals were low-pass filtered at 300 Hz, digitized at 1200 Hz and stored for off-line analysis. To measure the head position with respect to the axial gradiometers, three coils were placed at anatomical landmarks of the head (nasion, left and right ear canal). Head position was monitored in real-time (Stolk, Todorovic, Schoffelen, & Oostenveld, 2013).

2.5. Data preprocessing

Data was analyzed using the Fieldtrip software package, an open-source MATLAB toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). We analyzed the time window of -2 to 2 s relative to the SFWs (including 2 s after the SFW as well as the two immediately preceding words, i.e. SFW-1 and SFW-2). A third order synthetic gradiometer correction was applied to remove noise from the environment. Trials contaminated with muscle or MEG jump artifacts were identified and removed using a semi-automatic routine. After that, we performed independent component analysis (ICA; Bell & Sejnowski, 1997; Jung et al., 2000) to the data and removed ICA components associated with eye-movement and cardiac related activities from the MEG signals. Ultimately, we inspected the data visually and removed any remaining artifacts. In the end, on average 96% of trials were kept, with equal numbers of

trials (58 trials on average) among the four conditions (all *p*s > 0.19).

2.5.1. Time-Frequency Representations (TFRs) of gamma power

The TFRs of the single trials were calculated in the frequency range of 30 – 200 Hz using a multitaper approach (Mitra & Pesaran, 1999). Power estimates were computed with a 200 ms time-smoothing and a 10 Hz frequency-smoothing window, in 5 Hz frequency steps and 50 ms time steps. The TFRs were calculated at each sensor location for the vertical and horizontal planar gradient and then combined (Bastiaansen & Knösche, 2000). The planar gradient TFRs of the HC and LC conditions were averaged separately for each participant. The TFRs were log10 transformed and the power changes in the post-stimulus interval were expressed as an absolute change from the -1750 to -1250 ms baseline pre-stimulus interval (i.e. $\log_{10}(\text{Power}_{post}/\text{Power}_{pre})$. The baseline correction was conducted to visualize the induced gamma power (Fig. 1). No significant difference was found in the gamma power in the baseline period. Due to temporal smearing, any given time point in the resulting TFR is a weighted average of the time window of ±100 ms.

2.5.2. TFRs of R-values for the correlation between pre- and post-SFW gamma power

To examine whether the gamma activity is associated with representational-specific pre-activations, we correlated the gamma power induced by the SFWs (i.e. activation amplitude) with the gamma power associated with the prediction of the SFWs (i.e. prediction amplitude) across trials before baseline correction. We focused on the early stage of word encoding, such as visual word-form analysis (Hauk, Davis, Ford, Pulvermüller, & Marslen-Wilson, 2006; Leonard et al., 2013), such that the activation was estimated within the first 200 ms. This was done to isolate the brain activity that reflects the initial analysis of the presented words instead of the integration of the words with previous contexts (Kutas & Federmeier, 2011). If

gamma activity is associated with representational-specific pre-activations, the activation amplitude should more closely resemble the prediction amplitude when there was a strong prediction (i.e. HC/C) compared to when there was no clear prediction (i.e. LC/C and LC/IC) of upcoming words or a violation of the prediction (i.e. HC/IC). As shown in Fig. 2A, we first calculated the time-frequency representation (TFR) of gamma power for each trial (as described in *2.5.1.*). The gamma power values at the 100 ms time point (i.e. the weighted average of the gamma power in the 0 – 200 ms time window) reflected the activation amplitude in response to the SFWs. Likewise, the gamma power values between the -800 and -200 ms time window related to the prediction amplitude associated with the SFWs. We calculated Spearman correlations between the activation amplitude at 100 ms and the prediction amplitude at each time point in the -800 to -200 ms time window and each frequency point in the 50 – 100 Hz frequency band across trials, for each sensor and each participant. This resulted in a time-frequency representation of R-values for each sensor and each participant. We conducted this analysis separately for the trials of the four conditions. The time-frequency representation of R-values in the four conditions, as well as the difference between the HC/C and each of the HC/IC, LC/C, LC/IC conditions, are shown in Fig. 2B. The topographic distributions of the R-values in selected time and frequency windows (see *Results*) are shown in Fig. 2C.

2.5.3. Measure the gamma dominating frequency by calculating the center frequency of power

After establishing a link between gamma activity and representational-specific pre-activation, we further tested whether the frequency of the gamma activity differed between the four conditions. The frequency was quantified as *center of power* in the 50 – 100 Hz frequency range. We first estimated the gamma power spectrum by averaging the trial-averaged TFRs

over time (100 – 350 ms relative to the SFWs). Then the *center frequency of power* (CFoP) was calculated as $CFoP = \frac{\sum_{k=1}^{n} k \times power(k)}{\sum_{k=1}^{n} power(k)}$, where k represents the frequency, and power(k) represents the power at frequency k. This gave us an estimation of the dominating frequency within 50 – 100 Hz in the time window of 100 – 350 ms relative to the SFWs. We calculated the CFoP for six posterior sensors where the representational-specific gamma activity was most prominent (as circled in the topographic map in Fig. 2C). This was done separately for the four conditions for each participant. We compared the HC/C condition with the other three conditions, as the prediction was only confirmed in the HC/C condition whereas it was violated in the HC/IC condition and it was unpredictable in the LC conditions. In order to test whether the center frequency difference could be exclusively explained by the predictability of the SFWs, we also calculated the CFoP of the gamma activity induced by the pre-SFW between 100 – 350 ms after the SFW-1 was presented. The CFoP difference between conditions was statistically tested using ANOVA on the CFoP values over six posterior sensors, with two within-subject factors of Conditions (HC/C, HC/IC, LC/C, LC/IC) and Time windows (post-SFW, pre-SFW). Greenhouse-Geisser correction was applied when the degree of freedom in the numerator was larger than one. The original degrees of freedom with corrected p values was reported.

2.5.4. Cluster-based permutation statistics

We performed cluster-based permutation tests (Maris & Oostenveld, 2007) across participants for the TFR of power and the TFR of R-values. Based on previous MEG studies (Arnal et al., 2011; Todorovic et al., 2011) as well as visual inspection of the data, we statistically quantified the gamma power difference (Fig. 1) in the 60 – 90 Hz frequency band

between the four conditions both before (-1000 – 0 ms) and after (0 – 1000 ms) the presentation of the SFWs. As for the TFR of R-values (Fig. 2), we compared the R-values within 60 – 90 Hz frequency bands in the prediction period (-800 – -200 ms) relative to SFWs to avoid any contamination of the evoked responses to the pre-SFWs (which were presented during -1000 – -800 ms relative to SFWs). All sensors and time points were included into the permutation test initially. After identifying the time windows that showed significant effects, we averaged the data within the time interval and then the cluster was defined at the sensor level. A brief description of the cluster-based permutation test is as follows. First, for each data sample of the observed data (i.e., sensor or sensor by time data sample), we computed the mean difference between two conditions. Clusters were defined by the 95th percentile of the mean difference values, and the sum of the mean difference values within each cluster was calculated. Next, a null-distribution was created by randomly assigning the values to the two conditions 1000 times, with the largest cluster-level statistic in each permutation entering the null distribution. Finally, each observed cluster-level statistic was compared with the permutation distribution to assess significance for each cluster. Clusters falling in the highest or lowest 2.5th percentile were considered significant.

3. Results

Participants read highly constraining (HC) or low constraining (LC) sentences that ended with either congruent or incongruent words. They were asked to judge the correctness of statements in 20% of the sentences. Participants made highly accurate responses in all conditions [Mean (SD) = 98.7% (0.2%), 98.3% (0.3%), 98.3% (0.3%) and 97.6% (0.3%) respectively for the HC/C, HC/IC, LC/C and LC/IC conditions], suggesting that they carefully read the sentences for comprehension. The accuracy was slightly higher in the C than the IC condition, as indicated by a main effect of Congruency: $F_{(1,31)} = 4.394$, $p = .044$, η^2

= .124. No difference was found in the response time: Mean (SD) = 1318 ms (96 ms), 1330 ms (102 ms), 1298 ms (96 ms) and 1334 ms (102 ms) respectively for the HC/C, HC/IC, LC/C and LC/IC conditions, all *p*-values > .150.

The low-frequency power effects as well as the source localization results can be found in Wang, Hagoort, & Jensen (2017). Fig. 1A shows the gamma power induced by the sentence-final words (SFWs) and prefinal words (SFWs-1) in the four conditions after a baseline correction of -1750 to -1250 ms (i.e. preceding SFW-1). The visual presentation of words induced gamma power increase in the 100 – 350 ms time window after the words' onsets. A cluster-based permutation test conducted on the averaged gamma power in the 60 – 90 Hz across the 0 – 1000 ms interval revealed reduced gamma power in the HC/C than the HC/IC condition between 300 and 600 ms (p = .026). However, no gamma difference was found between HC/C and LC/C (p = .252) or between HC/C and LC/IC (p = 1.0) conditions. The results suggest that the gamma power induced by the expected words in the high-constraining contexts did not differ from the unexpected words in the low-constraining contexts. In addition, no gamma power difference was found before the SFWs were presented (all ps > .60), suggesting that the gamma power difference was not sensitive to the prediction difference.

* Insert Fig. 1 *

Previous studies have shown that pattern of gamma activity relates to item-specific representations (Polanía et al., 2012; Zhang et al., 2015), so it is very likely that the gamma activity associated with the activation of a specific word resembles the prediction of that word. In order to test this, we correlated the gamma power induced by the SFWs with the gamma power during the prediction period where no words were presented (i.e. -800 – -200

ms relative to SFWs). We hypothesized that if gamma activity relates to representational-specific prediction, the gamma power correlation between the activation period (around 100 ms) and the prediction period (-800 – -200 ms relative to the SFWs) should be stronger in the HC/C than in the other conditions. The cluster-based permutation test conducted to the -800 – -200 ms interval revealed a larger correlation in the gamma frequency band (60 – 90 Hz) for the HC/C condition compared to the HC/IC ($p = .022$), LC/C ($p = .008$) as well as LC/IC conditions ($p = .022$). Then we identified the time interval that showed significant effect (Fig. 2B) and averaged the R-values within the time interval for cluster-based permutation test at the sensor level to identify the sensors that showed significant effects (Fig. 2C). The larger correlation for the HC/C condition was found over posterior sensors (as marked by white asterisks in Fig. 2C) in the time interval of -650 – -600 ms, -700 – -650 ms, and -650 – -600 ms respectively for the HC/IC ($p = .002$), LC/C ($p = .002$), and LC/IC ($p = .004$) conditions. The highly significant effects indicate that the correlation difference between the HC/C and the other conditions was very robust. Since previous studies have also reported prediction modulation on the power of low frequency bands (2 – 30 Hz) (Dikker & Pylkkänen, 2013; Piai et al., 2016; Piai, Roelofs, & Maris, 2014; Piai, Roelofs, Rommers, & Maris, 2015; Rommers et al., 2016; Wang, Hagoort, & Jensen, 2017), we also conducted a similar correlation analysis to the low-frequency band. The statistical test between the HC/C condition and the other conditions (i.e. HC/IC, LC/C, LC/LC) did not yield any significant effect in the theta (3 – 8 Hz), alpha (8 – 12 Hz) or beta (15 – 20 Hz) frequency band, indicating that the correlation effect was specific to the gamma frequency band.

* Insert Fig. 2 *

Previous studies based on place recordings in the rat have shown that slow and fast frequencies of hippocampal gamma activity relate to prospective spatial representations

retrieved from memory and retrospective spatial representations reflecting the immediate past respectively. In the current study, the high-constraining context may have triggered prospective retrieval, which would predict more gamma power to be present at slower frequencies when comparing the HC/C to the other conditions. Indeed, using a *center-frequency-of-power (CFoP)* analysis, we found that the center frequency of the gamma activity was lower in the HC/C than the HC/IC ($t_{(31)} = 2.72$, $p = .010$), LC/C ($t_{(31)} = 2.56$, $p = .016$), and LC/IC ($t_{(31)} = 2.32$, $p = .027$) conditions: $F_{(3,93)} = 3.382$, $p = .026$, $\eta^2 = .098$ (Fig. 3A). The scatter plot of the CFoP of the HC/C condition against the other three comparing conditions confirmed this observation (Fig. 3B), showing that most participants had a slower dominating gamma frequency in the HC/C than the comparing conditions (points above the diagonal line). In order to test whether this was solely due to the predictability of the sentence-final words (SFWs), we also compared the CFoP of the gamma activity in the pre-SFWs interval between the HC/C and each of other conditions. The gamma activity in the pre-SFW interval showed no CFoP difference between HC/C and HC/C, LC/C or LC/IC conditions: $F_{(3,93)} = .612$, $p = .593$, $\eta^2 = .019$, as shown in Fig. 3C and Fig. 3D. The interaction test between Conditions (HC/C, HC/IC, LC/C, LC/IC) and Time window (SFW, pre-SFW) showed a marginally significant effect: $F_{(3,93)} = 2.570$, $p = .068$, $\eta^2 = .077$.

* Insert Fig. 3 *

4. Discussion

The current study examined gamma activity associated with language prediction when participants read sentences ending with expected words in high-constraining context (HC/C) or unexpected words in high-constraining context (HC/IC) or unexpected words in low-constraining contexts (LC/C and LC/IC). No consistent difference in gamma power was found between the HC/C and other conditions in either the prediction or activation time

windows. However, the gamma power in the prediction and activation time windows were more similar when the prediction was confirmed compared to when the prediction was violated or when no strong prediction could be made. In addition, the processing of expected words in the HC condition induced gamma activity with a slower frequency compared to the processing of unexpected words in the other conditions.

Unlike previous studies (Hagoort et al., 2004; Hald et al., 2006; Monsalve et al., 2014; Penolazzi et al., 2009; Rommers et al., 2013; Wang, Zhu, et al., 2012), the current study found no significant gamma power difference elicited by the expected words in the high-constraining contexts and the unpredictable words in the low-constraining contexts. It should be noted, however, that the violation of prediction (HC/IC vs. HC/C) produced stronger gamma activity in the high-constraining contexts between 300 – 600 ms. In addition, the test of congruency effect (HC/IC + LC/IC vs. HC/C + LC/C) revealed stronger gamma power in the incongruent than in the congruent conditions in the 150 – 650 ms interval ($p = .024$), as reported in our previous paper (Wang, Hagoort, & Jensen, 2017). As discussed in Lewis & Bastiaansen (2015), the mixed findings on the gamma power difference between the expected and unexpected inputs might be explained by a potential confound between prediction and attention. It has been shown that attended stimuli trigger stronger gamma-band responses than unattended stimuli (Bauer, Oostenveld, Peeters, & Fries, 2006; Gruber, Müller, Keil, & Elbert, 1999; Jensen & Colgin, 2007). Since it is difficult to disentangle prediction from attention (Summerfield & de Lange, 2014), and various factors can affect attention (such as the proportion of violating stimuli in the experiment and the task requirement), the lack of a consistent gamma power difference in the current study might be explained by the confound of attention.

By correlating the gamma power between the activation and prediction time windows across trials, we found that the gamma activity induced by processing the expected word was similar to the gamma activity induced by the prediction of that word in the HC/C condition. Previous studies have shown that remembered items induced gamma activity with similar spatial and temporal patterns between encoding and retrieval intervals (Zhang et al., 2015), and that specific information maintained in visual working memory can be decoded from gamma oscillatory patterns in the prefrontal cortex (Polanía et al., 2012). In the current study, gamma power in the post-stimuli and pre-stimuli time windows was related to item-specific activation and pre-activation respectively. We then correlated gamma power across trials separately for the HC/C, HC/IC, LC/C and LC/IC conditions. In the HC/C condition, the same word was pre-activated and processed, resulting in a high correlation of gamma power between the activation and prediction time windows. In the HC/IC condition, the perceived word differed from the predicted word, resulting in a weaker correlation. In the LC conditions, no specific word could be predicted, so the magnitude of gamma activity associated with the processing of the unexpected word did not resemble the magnitude of gamma activity during the prediction interval, also leading to a lower correlation of gamma power between the activation and prediction time windows. The effect was most robust during the -700 – -650 ms interval preceding the onset of the sentence-final words (SFW), which overlapped with the gamma activity induced by the pre-sentence-final words (SFW-1) in the -900 – -650 ms interval. It is very likely that the processing of the SFW-1 and the pre-activation of the SFW co-occurred. However, since the SFW differed from the SFW-1 across all conditions, the greater gamma power correlation between the pre- and post-stimuli intervals could only be attributed to the pre-activation of the highly predicted words. Moreover, this gamma correlation effect was mainly found in posterior regions (Fig. 2C), presumably over the visual cortex. It has been shown that people make predictions at the level of the visual/orthographic

features of upcoming words whenever it is possible (Brothers, Swaab, & Traxler, 2015; Dikker & Pylkkanen, 2011; Kim & Lai, 2012; Laszlo & Federmeier, 2011; Molinaro et al., 2013; Wang et al., 2017). The induced gamma activity around 100 ms after the onset of the SFW most likely reflects the visual processing of the presented words (Hauk, et al., 2006; Leonard et al., 2013). Therefore, the high correlation of gamma activity between the activation and prediction of the expected words in the HC/C condition might be due to predictions of the visual/orthographic characteristics of the lexical items.

The higher gamma power correlation between the prediction and activation periods in the HC/C than in the HC/IC, LC/C and LC/IC conditions seems to be consistent with the notion that gamma activity relates to the matching of pre-activation and processing of predicted words (Lewis et al., 2015), rather than reflecting prediction error (Arnal & Giraud, 2012; Friston et al., 2015). According to the predictive coding framework (Clark, 2013; Friston, 2011; Rao & Ballard, 1999), only the prediction error (i.e. the difference between the predicted and the perceived sensory input) is propagated to higher-level cortical regions. In the current study, the expected word matched the prediction, and thus the prediction error in the HC/C condition was minimal. If gamma activity relates to prediction error, which reflects brain activity that cannot be explained by the prediction, then the gamma activity induced by the expected word should not correlate with the gamma activity induced during the prediction period. We found that the processing of the expected word instead showed similar gamma power to the prediction of that word. Thus, our study provides support for the notion that gamma activity relates to the match between top-down prediction and bottom-up input.

In addition, we found that the expected words in the high-constraining contexts (i.e. the HC/C condition) induced gamma activity with a slower frequency than the unexpected words

in the high-constraining contexts (i.e. the HC/IC condition) as well as the words in the low-constraining contexts (i.e. LC/C and LC/IC conditions) did. That is, although the words in all conditions induced gamma activity, the gamma activity induced in the HC/C condition was dominated by relatively slower gamma activity compared to the other conditions. In the literature on hippocampal gamma activity, synchronization of slow gamma oscillations between CA3 and CA1 areas has been shown to reflect prospective representations of upcoming locations whereas synchronization of fast gamma oscillations have been related to retrospective representations reflecting the immediate past (Colgin et al., 2009; Bieri, Bobbitt, & Colgin, 2014; Colgin & Moser, 2010; Zhang et al., 2015). In the present study, the expected words in the HC/C condition – associated with slower gamma – could be retrieved from long-term memory and represented in a predicted/prospective manner. In contrast, the unexpected words in the HC/IC and LC conditions might be maintained temporarily in a retrospective manner to be integrated into the preceding contexts. Therefore, our finding on the relatively slower gamma in the HC/C condition than in the unexpected conditions parallels the rat hippocampal findings.

Overall, despite the lack of consistent gamma power difference between the expected (in the HC/C condition) and unexpected (in the LC conditions) words, the current study establishes a link between prediction and activation of highly expected words, as indicated by their strong correlation in gamma activity. In addition, it is the first study to report a lower dominating gamma frequency for expected words in the high-constraining context compared to unexpected words in language processing, supporting a functional distinction between slow and fast gamma oscillatory activity. Therefore, it is crucial to study various aspects of gamma oscillatory activity associated with language prediction.

5. Acknowledgments

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Figure legends

Fig. 1. Time-frequency representations (TFRs) of gamma power in four conditions at one left posterior sensor (MLO42), with relative power change compared to the baseline period (-1.75 – -1.25 s, not shown). The sentence-final word (SFW) started at 0 s. The presentation of words (-1 – -0.8 s and 0 – 0.2 s) induced gamma power increase in the 0.1 – 0.35 s time window relative to words' onsets. The gamma power showed strong posterior distribution, as shown in the topographic plots under the TFR plots. No significant gamma power difference was found between the HC/C and LC/C or LC/IC conditions in either the pre-SFWs or post-SFWs time interval. The gamma power was stronger in the HC/IC than the HC/C condition in the 300 – 600 ms interval relative to the onset of SFW over left temporal sensors. HC: highly constraining; LC: low constraining; C: congruent; IC: incongruent; SFW: sentence-final word.

Fig. 2. Correlation between induced gamma power during the pre- and post-SFWs time windows. (A) An illustration of the correlation analysis. First, the time series of all trials were transformed to time-frequency domains. The gamma power in the post-SFWs interval at 100 ms (the weighted gamma power in the time window of 0 – 0.2 s) reflected the activations in response to the SFWs, which served as reference gamma activity. The reference gamma activity (at 0.1 s) was correlated with the gamma power values at each time point (in the -0.8 – -0.2 s time window relative to the SFWs) and frequency data point (50 – 100 Hz) across trials. This resulted in a time-frequency representation of R-values for each sensor and each participant. The analysis was conducted separately for the trials in the HC/C, HC/IC, LC/C and LC/IC conditions. (B) Time-frequency representation of R-values in the four conditions as well as three contrasts: HC/C vs. HC/IC (left panel), HC/C vs. LC/C (middle panel), HC/C vs. LC/IC (right panel). The R-values were averaged over sensors that showed significant difference for each contrast. Between 60 – 90 Hz frequency, the correlation was stronger in the HC/C than the HC/IC, LC/C and LC/IC conditions during -0.65 – -0.6 s, -0.7 – -0.65 s, and -0.65 - -0.6 s time windows respectively. (C) The topographic distributions of the R-values in the frequency and time intervals that showed significant effects for the four conditions as well as the contrasting conditions. The sensors showing significant effects were marked by white asterisks. HC: highly constraining; LC: low constraining; C: congruent; IC: incongruent; SFW: sentence-final word.

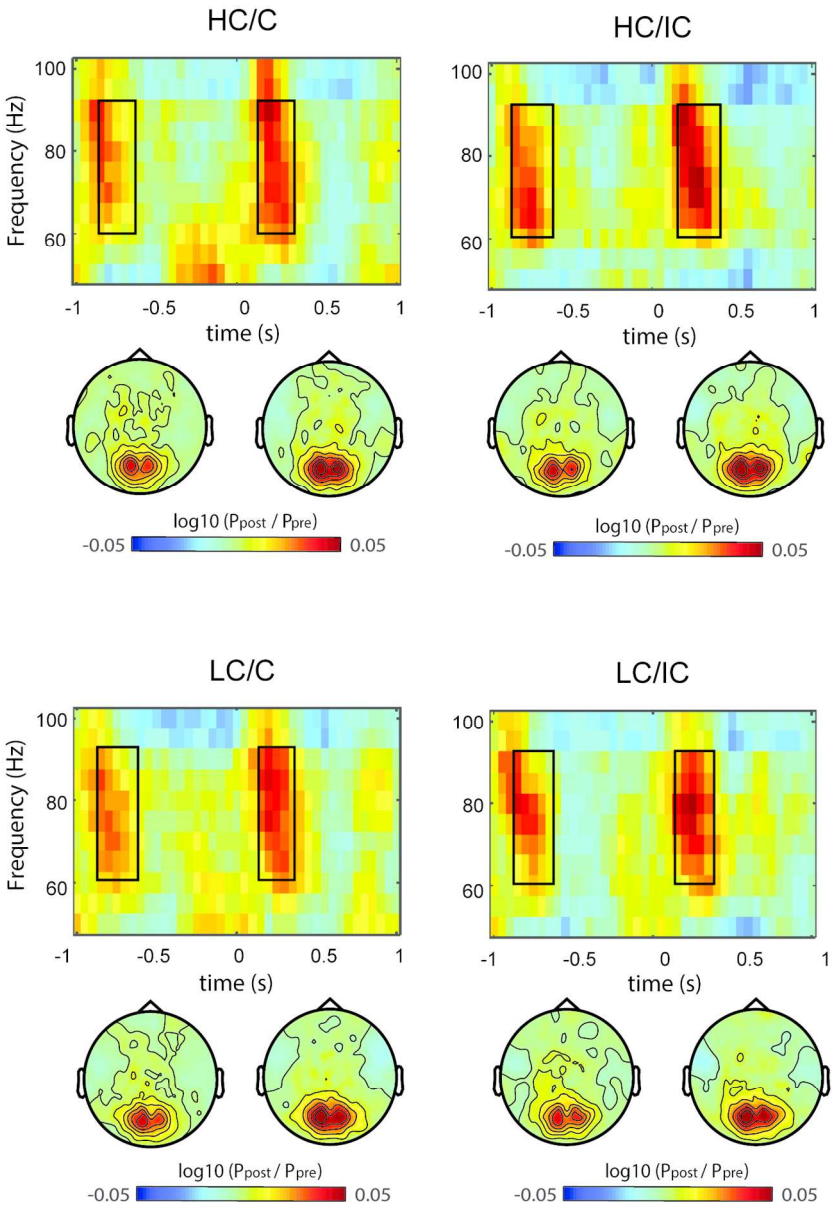
Fig. 3. Averaged gamma power spectrum in the 0.1 – 0.45 s time window over six posterior sensors (as circled in the first topographical map in Fig. 2C). (A) Gamma power spectrum averaged in the 0.1 – 0.35 s time window relative to the SFWs. The dominating gamma frequency in the HC/C condition was lower than that in the HC/IC, LC/C and LC/IC conditions. (B) Scatter plot of the center-frequency-of-power (CFoP) value in the HC/C condition versus that in the HC/IC (in red dot), LC/C (in blue dot) and LC/IC (in green dot) conditions in the post-SFWs interval for 32 participants. Most dots fall above the diagonal line, indicating that the CFoP values in the HC/C condition were smaller than those in the other conditions for most participants. (C) Gamma power spectrum in the 0.1 – 0.35 s time window relative to the pre-SFWs. The dominating gamma frequency in the four conditions showed no statistically significant difference. (D) Scatter plot of the center-frequency-of-power (CFoP) value in the HC/C condition versus that in the HC/IC (in red dot), LC/C (in blue dot) and LC/IC (in green dot) conditions in the pre-SFWs interval for 32 participants. The number of dots above and below the diagonal line was similar, suggesting no clear CFoP values difference between the HC/C and the other three conditions. HC: highly constraining; LC: low constraining; C: congruent; IC: incongruent; SFW: sentence-final word.

Table

Table 1. Examples of two items in four conditions.

1. High/Low constraining (HC/LC), Congruent/Incongruent (C/IC)
HC-C/IC: Hij gaf haar een **ketting** voor haar verjaardag/borstel.
(He gave her a **necklace** for her birthday/brush.)
LC-C/IC: Hij gaf haar een **ticket** voor haar verjaardag/borstel.
(He gave her a **ticket** for her birthday/brush.)
2. High/Low constraining (HC/LC), Congruent/Incongruent (C/IC)
HC-C/IC: Om de **cellen** te kunnen zien gebruikte hij een microscoop/kathedraal.
(In order to see the **cells** he used a microscope/cathedral.)
LC-C/IC: Om de **objecten** te kunnen zien gebruikte hij een microscoop/kathedraal.
(In order to see the **objects** he used a microscope/cathedral.)
Statement: Hij gebruikte een apparaat om iets te kunnen zien.
(He used a device in order to see something.)

Note: The examples were originally in Dutch, with the sentence-final words underlined. The critical words that create different contextual constraints were in bold. The target words were underlined. The English translations are given in brackets below the original Dutch materials. An example of the statement (which required YES answer) was provided for example 2.



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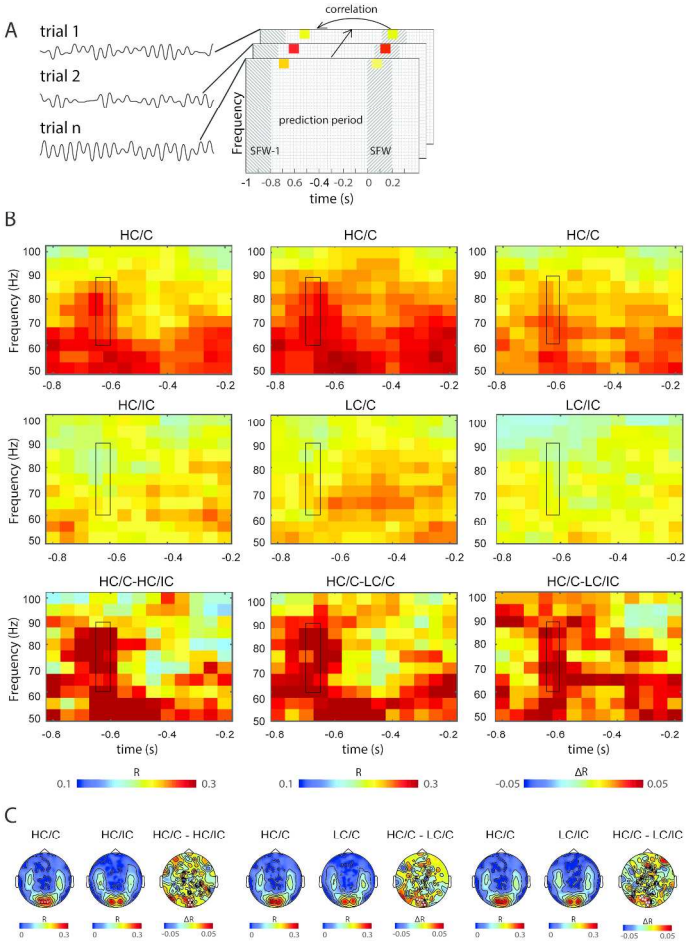
120x174mm (300 x 300 DPI)



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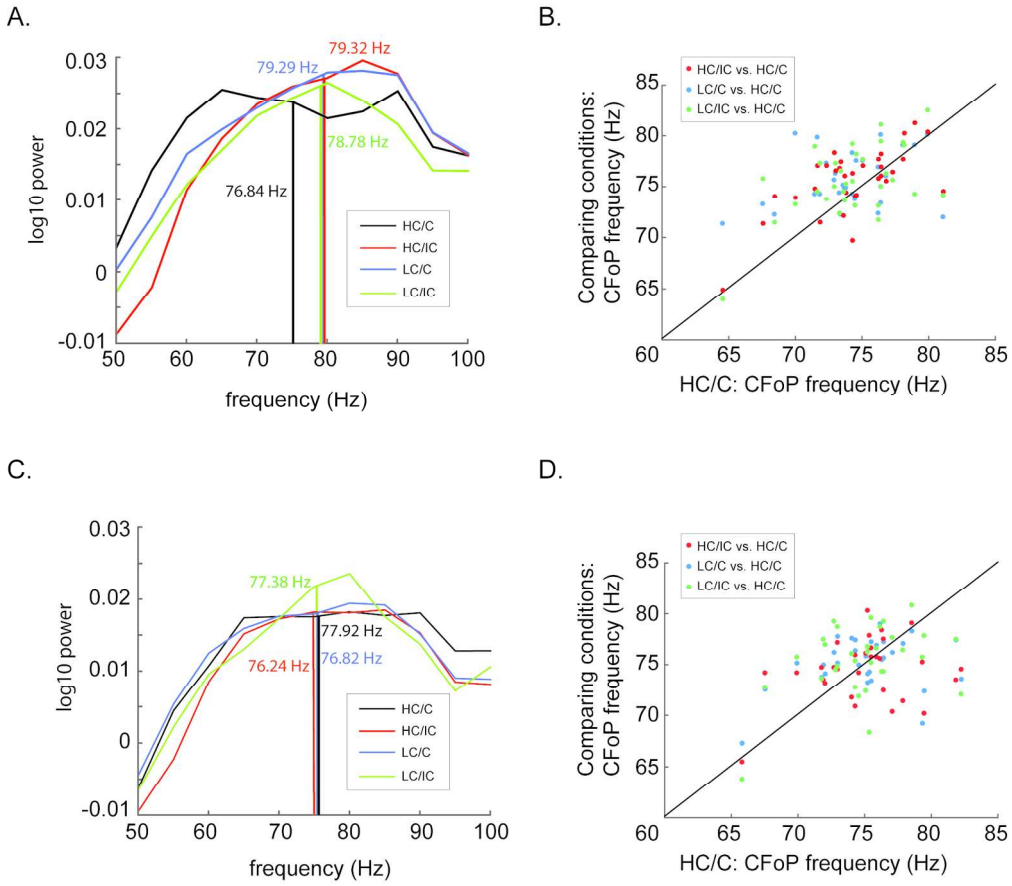
254x238mm (300 x 300 DPI)



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163x143mm (300 x 300 DPI)